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Reconstructing the thermal history of fish juveniles using stable oxygen isotope analysis of otoliths

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Introduction: Characterizing the thermal habitat of fish is key to understanding their ecological requirements in order to make appropriate management plans for the preservation of fish populations in the context of climate change. Little is known about the thermal habitat of the early life stages of fish (larvae and juveniles), as most methods have been designed for large, easily handled individuals. In particular, the study of otoliths holds great promise for unveiling the early thermal history of fish, although it is challenging to implement due to the very small size of the biological material.

Methods: The stable oxygen isotope content ($\delta^{18}O$) of biogenic carbonates (such as otoliths) can be used to reconstruct the life temperature of fish individuals. However, relationships between $\delta^{18}O$ of otoliths and ambient temperature are scarce and mainly developed for commercial species. In this study, we assessed the $\delta^{18}O$ of juvenile European chub (*Squalius cephalus*, Linnaeus 1758) living in a section of the lower Rhône River in France.

Results: The $\delta^{18}O$ of otoliths showed significant relationship with ambient temperature [$\delta^{18}O_{oto(VPDB)}$ - $\delta^{18}O_{w(VPDB)}$ = 33.391 − 0.2641 * T (°C)], and the relationship between temperature and the fractionation factor (α) was $1{,}000 \ln \alpha = -43.472 + 21.205\ [1{,}000/T(K)]$.

Discussion: As expected, back-calculated temperatures from these equations were in much better agreement with the measured *in situ* temperatures than previously published equations. This equation is the first to be developed for leuciscid fish in Europe and the second in the world.

KEYWORDS

water temperature, fractionation equation, European chub, *Squalius cephalus*, Rhône river

1 Introduction

Among environmental parameters, water temperature plays a major role in physiological processes and life history traits of ectotherms (Magnuson et al., 1979; Van Der Have and De Jong, 1996; Małek et al., 2015) and this is especially true for fish (Payne et al., 2016). Temperature, along with physical factors, determines both the regional distribution (Buisson et al., 2008) and the fine-scale habitat requirement during ontogenesis of fish species (Schiemer et al., 2004). All these processes act on the fitness of individuals and determine their thermal niche. The thermal niche of ectotherms corresponds to the temperature conditions suitable for an organism to grow, feed, and reproduce, and it can differ between life stages (Hutchinson, 1957; Magnuson et al., 1979). According to a review by Gvoždík (2018), the thermal niche of a species has usually been determined using one of the following approaches: 1) by measurements of the thermal dependence of life history traits, 2) from laboratory experiments under controlled conditions to obtain thermal preferenda, or 3) by modelling biogeographic distributional. However, several studies have shown that the temperatures obtained using these approaches may differ from the *in situ* requirements of the species (e.g., Schrank et al., 2003). Therefore, a tool able to assess the thermal niche realized by individuals is required to identify essential habitats (Morrongiello et al., 2012).

In situ temperature measurements are often one-off in space and time and could be significantly different to the thermal habitat inhabited by individuals during the different stages of their life cycle. This is particularly true in large floodplain rivers, where the temperature of aquatic habitats used by fish is highly variable in space and time, both within the channel cross section and between waterbodies (Tonolla et al., 2012). For example, lithophilic riverine species show habitat shifts during their early life, from lotic gravel spawning grounds during embryogenesis and lentic inshore microhabitats used by larvae to more lotic and deeper waters for juveniles. This illustrates that individuals are exposed to contrasting thermal conditions throughout their life, most notably in their early life stages. In such conditions, reconstructing the thermal life history of fishes is challenging and requires methodological developments.

The lack of basic information on the actual thermal conditions experienced by aquatic ectotherms makes the determination of their thermal niche particularly imprecise. Many studies used data storage tags implanted directly on individuals to continuously record the water temperature of their immediate environment (e.g., Pálsson and Thorsteinsson, 2003; Hunter et al., 2004). However, such a tagging approach requires a minimum body length (and weight) of individuals to support this equipment, thus excluding larvae and small fish (juveniles or small-sized species). Natural proxies that accurately record the environmental conditions in which organisms lived could be an alternative solution. Among them, the isotopic signature of biogenic carbonates has often been used.

Otoliths are calcium carbonate structures of the inner ear of teleost fish that are metabolically inert (no dissolution or resorption) and grow throughout the life of the fish (see, Campana and Neilson, 1985; Campana, 1999; Campana and Thorrold, 2001). They form growth increments (daily and seasonal) and their chemical composition reflects the chemical composition of the surrounding water, fish diet, and metabolic rate (Campana, 1999). Otoliths are used notably for reconstructing environmental exposure (Elsdon and Gillanders, 2002, 2004). Among key environmental parameters, the reconstruction of thermal exposure history of individuals is of growing scientific interest in the context of climate change (Morissette et al., 2023). This topic is particularly relevant for better understanding the use of thermally changing habitats by individuals, for characterizing behavioral adaption of organisms and for developing appropriate local restoration measures that take account of the gradual rise in temperature. Most studies that have focused on the reconstruction of thermal history of organisms have considered the stable isotopic composition of oxygen in the otolith as a temperature-dependent tracer linked to both the stable isotopic composition of oxygen in the water and ambient temperature (Patterson et al., 1993; Thorrold et al., 1997). The oxygen isotope signature in otoliths has been used to reconstruct the thermal life history of fish in paleontological studies (Andrus et al., 2002; Surge and Walker, 2005; Price et al., 2009; West et al., 2012) as well as in contemporary ecological studies in freshwater and marine environments (Thorrold et al., 1997; Blamart et al., 2002; Darnaude et al., 2014; Gerdeaux and Dufour, 2015; Burbank et al., 2020; Nazir et al., 2023).

Temperature reconstruction from biogenic carbonates is based on thermodynamic predictions at equilibrium of the oxygen isotope ratio ($^{18}O/^{16}O$) between newly formed calcium carbonate and the surrounding environment (e.g., water). This fractionation at equilibrium is determined by thermodynamic properties of exchange between phases, but the natural mineral growth can create a disequilibrium (Watkins et al., 2013; Daëron et al., 2019). For oxygen isotopes, this shift from equilibrium can be interpreted in terms of the kinetic effect during otolith formation and during the exchange of isotopes between the different species of dissolved carbon dioxide and water involving hydration and hydroxylation processes (see Mcconnaughey, 1989).

For decades, the estimation of the living temperature of fish from their $\delta^{18}O$ values (i.e., the relative variation of the ratio between ^{18}O and ^{16}O to a standard) of otoliths has been made using empirically determined equations (e.g., Thorrold et al., 1997; Darnaude et al., 2014; Burbank et al., 2020 and references therein). These equations have mainly been established on *sagittae* of fish species of commercial interest (mainly gadid and salmonid species). However, for the second-largest superorder of fish, Ostariophysi (which includes the species-rich orders Cypriniformes and Siluriformes), the fragility and the small size of their *sagittae* make their analysis tricky, if not impossible. The alternative solution that is usually opted for is to use the *lapillus*, the biggest otolith of Ostariophysi (e.g., Panfili et al., 2002; Bounket et al., 2019). To date, only two dedicated studies have looked at the oxygen isotope signature of *lapilli*. Smith and Jones (2006) in their study of *Cynoscion nebulosus* (Cuvier, 1830), a sciaenid juvenile, showed that *sagittae* and *lapilli* were not isotopically interchangeable, with an enrichment in $\delta^{18}O$ of 0.44‰ on average for *sagittae* compared to *lapilli*. In a recent study, Burbank et al. (2020) developed an empirical oxygen isotope fractionation equation for *Notropis photogenis* (Cope, 1865), a North American leuciscid. They have shown that it is possible to work on the *lapillus* of small fish, and they provide a more realistic back-calculated temperature using the equation they developed compared to those found in the literature.

The Cypriniformes (minnows, carps, loaches and suckers) comprising around 4,300 species represent 6% of all vertebrate species and one third of freshwater fish species (Stout et al., 2016). The phylogeny of this order was recently resolved using molecular analyses, and some groups previously classified in the Cyprinidae family were elevated in family level, such as the Leuciscidae, the Danionidae, and the Gobionidae, for example,

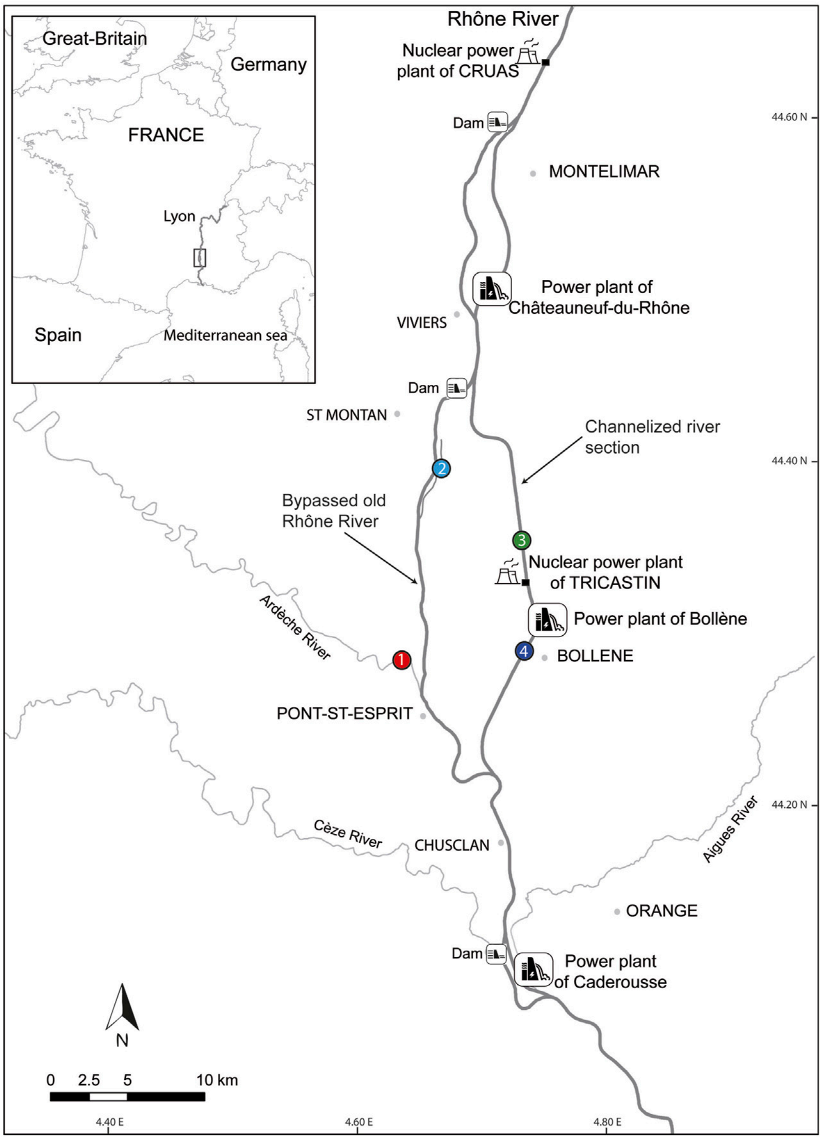

FIGURE 1
Map of the reach of Caderousse on the lower Rhône River. Water and fish were sampled at four stations: 1—the Ardèche River; 2—a backwater of the Rhône River—the lône de Malaubert; 3—the upstream section of the Tricastin nuclear power plant; and 4—downstream section of the Bollène hydroelectric power plant.

(Stout et al., 2016). To our knowledge, the equation developed by Burbank et al. (2020) is the only one specifically developed using the *lapillus* and considering a species from the Cypriniformes order. Understanding the relationship between temperature and the stable oxygen isotopic composition for other Cypriniformes from other freshwater hydrosystems is important for this overlooked order of fish. The European chub *Squalius cephalus* (Linnaeus, 1758), a potamodromous lithophilous species inhabiting both lotic and lentic freshwaters, is one of the most abundant and widespread Cypriniformes in Europe. This euryceous species lives in environments covering a wide range of temperatures. This makes it a relevant biological model to study the relationship between ambient temperature and the oxygen isotope signature of the *lapillus*, which would then be valid and applicable over a wide temperature gradient.

The aim of this study was first to estimate the relationship between the oxygen isotopic signature of *lapillus* and the mean temperature of the water in which juveniles have lived (i.e., over 3–6 months), and second to develop an empirical oxygen isotope fractionation equation valid for European chub. Finally, the performance of the identified relationship was assessed by comparison with other equations from the literature. This study was conducted on the reach of Caderousse (France), which is a 50-km-long section of the lower Rhône River. In this reach a previous study analyzed the microchemistry of water and chub otoliths and found that 70% of the young-of-the-year individuals sampled did not spread far away from their hatching area and can be considered as resident fish (Bounket et al., 2021). These individuals are therefore good candidates for studying the relationship between ambient temperature and the stable oxygen isotope content of otoliths in natural environments.

2 Material and methods

2.1 Study area

The study area is the reach of Caderousse, which is located between Montélimar and Orange on the lower Rhône River in south-eastern France (Figure 1). The reach of Caderousse is constituted by the two hydropower schemes of Donzère-Mondragon and Caderousse. This reach includes the by-passed section of the Donzère-Mondragon scheme, the reservoir of Caderousse, and the tailrace of the Bollène power plant. The by-passed section presents in its upstream part the lône de Malaubert, a backwater of the old Rhône River, and in its downstream part the confluence with the Ardèche River (a large typical Mediterranean tributary). The channelized section of the Donzère-Mondragon scheme receives heated cooling water on its right bank from the nuclear power plant of Tricastin. Four stations with contrasting thermal conditions were studied (Figure 1): 1) the Ardèche River at Pont-Saint-Esprit; 2) the lône de Malaubert; 3) a channelized section located upstream of the Tricastin nuclear power plant; and 4) a channelized section located downstream of the power plant of Bollène. Station 4 is located downstream of the release of heated cooling water from the Tricastin nuclear power plant, after complete mixing with the cooler water of the river.

2.2 Water sampling

Water was sampled monthly from February to December 2016 to assess the temporal variation in oxygen isotopes of the Rhône River, the lône de Malaubert, and the Ardèche River. Water was sampled close to the riverbank at depths between 0.5 and 1.0 m; this habitat and depth correspond to typical juvenile habitats. A glass vial (150 mL) was rinsed several times using the river water before being filled and sealed underwater and then sent for stable oxygen isotope analysis.

Each station was equipped with HOBO® thermometers that recorded temperature every 15 min. Daily water temperature averages were then calculated for each station.

2.3 Fish sampling

Fish juveniles were collected by electrofishing in the reach of Caderousse (from 29 November to 2 December 2016) and their origin, i.e., resident or migrant, was determined using otolith and water microchemical analyses (Bounket et al., 2021). For reasons of feasibility, we focused on the juvenile stage (individuals aged between 3 and 6 months). Fish were considered as resident (*i.e.*, individuals that were born and spent most of their life in the same environment where they were caught) if no significant difference was observed between the microchemistry of their otolith and the water microchemistry of the station where the fish were caught (see Bounket et al., 2021 for details). Among the fish used for the connectivity study by Bounket et al. (2021), 97% from the Ardèche River (30 out of 31 fish analyzed in station 1), 93% from the lône de Malaubert (28/30 in station 2), 20% from the upstream section of the Tricastin nuclear power plant (3/15 in station 3), and 37% from the downstream section of the Bollène hydroelectric power plant (3/8 in station 4) were identified as residents. Among these resident fish, 39 individuals were used for stable isotope analyses in order to evaluate the ability of *lapilli* to record water temperature (Table 1). In this study, the resident fish were used because they are the only fish for which the thermal life history can be verified and compared with *in situ* temperature. Indeed, contrary to migrant fish that have inhabited different environments during their life, resident fish have lived in the same environment throughout their life.

2.4 Otolith growth rate

The growth rates of right otoliths were estimated based on the method described in previous studies (Bounket et al., 2019, 2021; Logez et al., 2021). Briefly, to expose the daily increments, the otolith was embedded in epoxy resin (Araldite 2020) and ground along the frontal plane using abrasive papers and diamond solutions. After digitization of the otolith, daily age and growth were estimated along a unique reading transect following the maximum growth axis. Fish age was estimated by counting the number of growth increments, and the growth rate was determined by measuring the distance between consecutive growth increments.

2.5 Stable isotope analysis

The left *lapillus* was used for the stable oxygen isotope analysis [the right *lapillus* was used for microchemistry and age analyses in Bounket et al. (2021)]. *Lapilli* were cleaned and baked at 380°C under vacuum for 45 min to avoid possible contamination by organic matter. Since chub *lapilli* are small, *in toto* analyses were performed from approximately 70 µg of otolith. All isotope analyses were carried out on an IRMS (isotopic ratio mass spectrometer) VG-OPTIMA coupled with an automated line of samples prepared in the “Laboratoire des Sciences du Climat et de l’Environnement (LSCE, Gif-sur-Yvette, France).” The results are given in the conventional (δ ‰) notation expressed in per mil against the VPDB (Vienna Pee Dee Belemnite) standard using Eq. 1:

$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 10^3 \quad (1)$$

where R_{sample} and $R_{standard}$ are the isotopic ratio $^{18}O/^{16}O$ of the sample and the standard, respectively. The reproducibility calculated from the calcite internal standard was 0.07‰ (1σ) for the oxygen.

The water samples were analyzed by cavity ring-down spectroscopy (CRDS) using a l2130i isotope and gas concentration analyzer (Picarro machine) at the LSCE. The samples (2 µL) are automatically injected into a vaporization module at 110°C before

TABLE 1 Number of resident fish, total fish length (LT in mm), and estimated fish age (in days) by station.

Sampling location	n	TL (mm)		Age (*d*)	
		min – max	Mean ± sd	min – max	Mean ± sd
Station 1—Ardèche River	22	33–67	49.9 ± 10.2	85–148	123 ± 17
Station 2—Lône de Malaubert	12	30–79	49.7 ± 14.2	68–173	130 ± 10
Station 3—Upstream of Tricastin PP	3	63–71	52.7 ± 5.7	103–128	118 ± 13
Station 4—Downstream of Bollène PP	2	30–79	67.0 ± 5.7	114–133	123 ± 13

PP, power plant.

being sent into the laser cavity. The time needed to measure a sample is 9 min. The CRDS device is calibrated daily by measuring two in-house standards (themselves calibrated against the international standards SMOW and SLAP) whose isotopic compositions frame the samples to be measured. The oxygen isotope compositions are given against the SMOW standard and the external precision of the measurement (1s) is 0.2‰.

2.6 Isotopic fractionation

Since studies on the isotopic signatures of *lapilli* were scarce, isotopic fractionation must first be tested before being established. The isotopic fractionation is a modification of the ratio between both heavy and light isotopes during a chemical reaction or a state change, which are influenced by temperature. The theoretical values in $\delta^{18}O$ of aragonite ($\delta^{18}O_{ara}$) for each month were determined using Eq. 2 from Watkins et al. (2013). This equation was determined experimentally and enables the calculation of the isotopic values of $\delta^{18}O$ considering the isotopic equilibrium between water and carbonate (without vital effect, i.e., without any influence of the organism metabolism or physiology on the mineralization). Although this equation was established for calcite, Lécuyer et al. (2012) concluded that biogenic calcium carbonate polymorphs precipitate with δ^{18}O values very close to each other and not far away from isotopic equilibrium with seawater. Then, these theoretical $\delta^{18}O_{ara}$ values were weighted by the fish life span ($\delta^{18}O_{oto\text{-}weighted}$) and compared with the values of $\delta^{18}O$ measured in otoliths ($\delta^{18}O_{oto}$).

$$\text{Watkins equation'}: \delta^{18}O_{ara} = \left(17.747 \times \frac{10^3}{T} - 29.777 + \delta^{18}O_w\right) \times 0.97001 - 29.29 \tag{2}$$

where T is the temperature in Kelvin and $\delta^{18}O_w$ the isotopic signature of the water expressed in SMOW.

For example, the $\delta^{18}O_{ara\text{-}weighted}$ of a fish aged 61 days, born on the 1 August and captured on 30 September, is obtained as shown in the mass balance Eq. 3.

$$\delta^{18}O_{ara-weighted} = \frac{31}{61} \times \delta^{18}O_{ara-August} + \frac{30}{61} \times \delta^{18}O_{ara-september} \tag{3}$$

Secondly, the otolith fractionation, the difference between the otolith and water $\delta^{18}O$ values, was plotted against the inverse of the average weighted temperature. These two parameters were linked using Eq. 4:

$$\delta^{18}O_{oto\,(VPDB)} - \delta^{18}O_{w\,(VPDB)} = a + b \times T\,(^\circ C) \tag{4}$$

where $\delta^{18}O_{oto\ (VPDB)}$ and $\delta^{18}O_{w\ (VPDB)}$ are the isotopic signatures of the otolith and water, respectively, expressed in VPDB, and a and b the coefficient of the linear regression. $\delta^{18}O_{w\ (VPDB)}$ values were obtained using Eq. 5:

$$\delta^{18}O_{w\,(VPDB)} = -29.98 + 0.97002 \times \delta^{18}O_{w\,(SMOW)} \tag{5}$$

In the literature, the fractionation equation derives from a fractionation factor (α) as shown in Eq. 6.

$$\alpha = \frac{\delta^{18}O_{oto\,(VPDB)} + 1000}{\delta^{18}O_{w\,(VPDB)} + 1000} \tag{6}$$

Individual values of α expressed in 1,000 ln (α) were plotted against the inverse of the average temperature T expressed in Kelvin. This Arrhenius diagram allows one to obtain a species-specific equation linking these two parameters, as shown in Eq. 7:

$$1000 \ln \alpha = c + d \times \left(\frac{1000}{T}\right) \tag{7}$$

where c and d are the coefficients of the linear relation.

2.7 Back-calculation of the temperature

The efficiency of the empirically established oxygen isotopic fractionation equation specifically defined for the European chub was evaluated by comparison to the back-calculated temperature obtained using nine equations from the literature and to the average weighted temperature from *in situ* measurement of each fish ($T_{weighted}$).

$$\Delta T = T_{weighted} - T_{cal} \tag{8a}$$

where $T_{weighted}$ is the average temperature of the sample location calculated from the monthly temperature weighted by the life span of each individual, expressed in °C. The T_{cal} is the back-calculated temperature using equations from the literature (Table 2).

2.8 Statistical analysis

Kruskal-Wallis non-parametric tests were used to compare 1) the mean annual temperature, 2) the $\delta^{18}O_w$, and 3) the $\delta^{18}O_{oto}$ between sites. Linear regressions were used to determine 1) the

TABLE 2 Equations of oxygen isotopic fractionation obtained from the literature and investigated in the present study.

Biological model	Equation	Environment	References
Experimental precipitation	$1000 \ln \alpha = -31.14 + 17.88 \times \left(\frac{1000}{T}\right)$	*In vitro*	Kim et al. (2007)
Experimental precipitation	$1000 \ln \alpha = -29.78 + 17.75 \times \left(\frac{1000}{T}\right)$	*In vitro*	Watkins et al. (2013)
Micropogonias undulatus	$1000 \ln \alpha = -32.54 + 18.56 \times \left(\frac{1000}{T}\right)$	Marine	Thorrold et al. (1997)
Gadus morhua	$1000 \ln \alpha = -27.09 + 16.75 \times \left(\frac{1000}{T}\right)$	Marine	Høie et al. (2004)
Boreogadus saida	$1000 \ln \alpha = -30.54 + 17.49 \times \left(\frac{1000}{T}\right)$	Marine	Kastelle et al. (2022)
Eleginus gracilis	$1000 \ln \alpha = -18.44 + 14.06 \times \left(\frac{1000}{T}\right)$	Marine	Kastelle et al. (2022)
Gadus macrocephalus	$1000 \ln \alpha = -17.41 + 13.57 \times \left(\frac{1000}{T}\right)$	Marine	Kastelle et al. (2022)
Theragra chalcogramma	$1000 \ln \alpha = -22.09 + 14.90 \times \left(\frac{1000}{T}\right)$	Marine	Kastelle et al. (2022)
Pleuronectes platessa	$1000 \ln \alpha = -24.25 + 15.99 \times \left(\frac{1000}{T}\right)$	Marine/brackish	Geffen (2012)
Anguilla rostrata	$1000 \ln \alpha = -18.65 + 14.30 \times \left(\frac{1000}{T}\right)$	Brackish/freshwater/marine	Holden et al. (2022)
Hypomesus transpacificus	$1000 \ln \alpha = -34.56 + 18.39 \times \left(\frac{1000}{T}\right)$	Freshwater/brackish	Willmes et al. (2019)
Salvelinus spp.	$1000 \ln \alpha = -41.69 + 20.69 \times \left(\frac{1000}{T}\right)$	Freshwater	Storm-Suke et al. (2007)
Salvelinus alpinus	$1000 \ln \alpha = -41.14 + 20.43 \times \left(\frac{1000}{T}\right)$	Freshwater	Godiksen et al. (2012)
Notropis photogenis	$1000 \ln \alpha = -34.38 + 18.42 \times \left(\frac{1000}{T}\right)$	Freshwater	Burbank et al. (2020)
Squalius cephalus	$1000 \ln \alpha = -43.47 + 21.21 \times \left(\frac{1000}{T}\right)$	Freshwater	This study

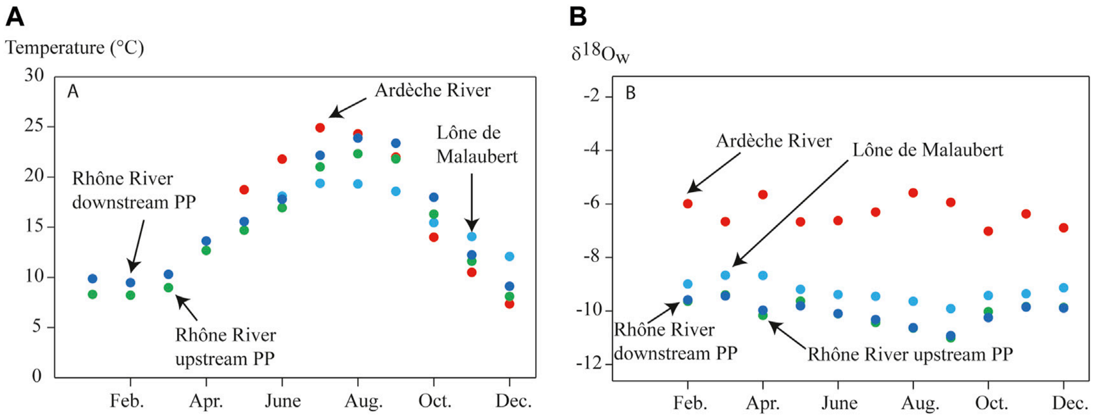

FIGURE 2
(A) Monthly water temperatures and **(B)** monthly oxygen isotope signatures of the water ($\delta^{18}O_{w\ \mathrm{SMOW}}$) measured at the four sampling stations. PP, power plant.

relationship between the fractionation factor and the temperature, and 2) the relationship between the temperature and the difference between the isotopic signature of otoliths ($\delta^{18}O_{oto}$) and water ($\delta^{18}O_{w}$). Spearman's correlation test was used to examine the relationship between $\delta^{18}O_{oto}$ and the average daily otolith growth rate, which is a proxy for average fish growth. The differences between the oxygen isotope signatures measured in otoliths and obtained theoretically were tested using the Friedman non-parametric test (χ^2). Similarly, the differences between back-calculated temperatures from the 14 equations were also tested using the Friedman non-parametric test (χ^2). The Friedman test was coupled with the Wilcoxon *post hoc* test to test for the significance of pairwise differences between equations. The size effect was assessed using the Kendall test (W). Kendall's W varied from 0 (weak effect) to 1 (strong effect). All analyses were performed with the software R (v. 3.6.2) and the libraries "stats" and "rstatix."

TABLE 3 Mean and standard deviation (sd) of the difference between $\delta^{18}O$ measured in otolith and theoretical values calculated using the equation from Watkins et al. (2013) and weighted by fish lifetime.

Stations	Mean (‰)	sd (‰)
Station 1—Ardèche River	−2.244	0.194
Station 2—Lône de Malaubert	−2.164	0.647
Station 3—Upstream of Tricastin power plant	−2.452	0.106
Station 4—Downstream of Bollène power plant	−2.362	0.014

3 Results

3.1 Temperature and oxygen isotope signature of water

All stations showed a marked seasonality in water temperature (Figure 2A), with no significant difference in monthly averages between stations ($\chi^2 = 2.69$, df = 3, $p = 0.44$). The coolest water temperatures were observed in December for all stations, while the warmest month varied between stations: July for the Ardèche River and the lône de Malaubert, and August for the stations located upstream of the Tricastin power plant and downstream of the Bollène power plant.

The isotopic signatures of oxygen ($\delta^{18}O_w$) differed significantly among stations ($\chi^2 = 32.97$, df = 3, $p = 3.27*10^{-7}$, Figure 2B). The Ardèche River showed the highest $\delta^{18}O_w$ values from −7.02 to −5.59‰, the lône de Malaubert showed intermediate values from −9.91 to −8.66‰, and the stations located upstream of the Tricastin power plant and downstream of the Bollène power plant showed the lowest values from −11.00 to −9.40‰ and from −10.99 to −9.44‰, respectively. The low $\delta^{18}O_w$ values of the Rhône River reflect the input throughout the year of ice-snow melted water from Lake Geneva.

3.2 Isotopic equilibrium and fractionation

Measured $\delta^{18}O_{oto}$ signatures were lower than theoretical values of calcium carbonate by −2.24‰ ± 0.39‰ on average [Friedman test χ^2 (1) = 39, $p = 4.24*10^{-10}$]. This value is 37% lower than the average $\delta^{18}O$ theoretical value. Although varying slightly among stations (Table 3), this difference suggests that the crystallization of calcium carbonate in lapilli is not in equilibrium with water, as the theoretical $\delta^{18}O$ values are derived from the Watkins equation (without vital effect).

The difference between the otolith and water $\delta^{18}O$ values showed a negative linear relationship with temperature ($F_{1,2} = 17.69$, $p < 0.05$) (Figure 3A, Eq. 8b).

$$\delta^{18}O_{oto\,(VPDB)} - \delta^{18}O_{w\,(VPDB)} = 33.391 - 0.2641 \times T\,(^\circ C) \tag{8b}$$

The fractionation factors expressed in 1,000 ln α showed significant differences between stations (Friedman test χ^2 = 13.889, df = 3, $p = 0.003$). A linear relationship was found with the weighted water temperature (expressed in Kelvin) ($F_{1,2} = 19.04$, $p = 0.048$) (Figure 3B, Eq. 9).

$$1000 \ln \alpha = -43.472 + 21.205 \times \left(\frac{1000}{T}\right) \tag{9}$$

No significant relationship was found between $\delta^{18}O_{oto}$ signatures and average daily otolith growth rates (Spearman correlation test, $\rho = 0.304$, $p = 0.06$; Figure 4) and between $\delta^{18}O_{oto}$ signatures and fish age (Spearman correlation test, $\rho = -0.09$, $p = 0.58$).

3.3 Temperature back-calculation

Based on the measured temperature weighted by the lifetime of fish, significant differences were observed for the average temperature experienced by fish among stations (KW $X^2 = 11.22$, df = 3, $p = 0.01$). The lowest values were observed in the lône de Malaubert (station 2), intermediate values in the Ardèche River (station 1) and in the upstream section of the Tricastin power plant

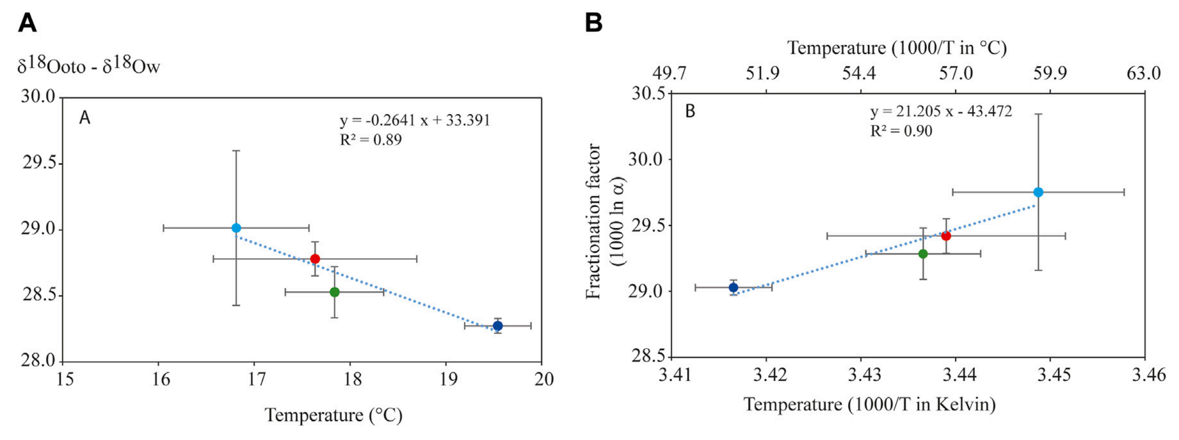

FIGURE 3
(A) Relationship between mean water temperature (T°C) weighted by each fish lifetime and otolith fractionation expressed as the difference between otolith and water $\delta^{18}O$ values ($\delta^{18}O_{oto} - \delta^{18}O_w$). **(B)** Relationship between isotopic fractionation expressed in 1,000 ln α and the mean water temperature weighted by fish lifetime (expressed in 1,000/T in Kelvin or °C). Error bars represent the standard deviation. Ardèche River station (red), lône de Malaubert (light blue), upstream of the Tricastin power plant (green), and downstream of the Bollène power plant (dark blue).

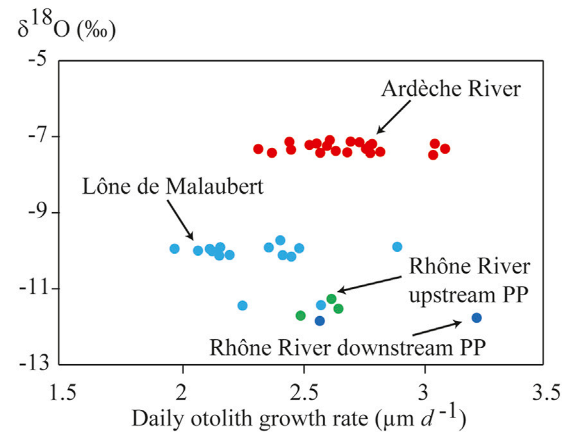

FIGURE 4
Relationship between the $\delta^{18}O_{oto}$ and the average daily growth rate of otoliths.

(station 3), and the highest values were found in the downstream section of the Bollène power plant (station 4) (Table 4).

Back-calculated temperatures estimated from fractionation equations strongly varied depending on the equation used (Friedman test χ^2 (10) = 380, $p < 0.01$, Table 4) with a large size effect (W = 0.974). All pairwise comparisons showed highly significant differences (Wilcoxon-tests, $p < 0.0001$) except in two cases. Non-significant differences were measured between the average weighted temperature and two equations: the one developed in the present study and the equation developed by Storm-Suke et al. (2007). The highest ΔT values were observed for back-calculated temperatures obtained from the Watkins et al. (2013) (−8.8°C) and the Thorrold et al. (1997) equations (−8.5°C) (Figure 5). The lowest ΔT values were obtained with the equation developed in this study (+0.01°C) and the one from Storm-Suke et al. (2007) (−0.02°C). The other equations yielded intermediate values (see Table 4 for the complete results).

Back-calculated temperature values obtained from the chub-specific equation showed that the sampled individuals had lived in distinct thermal habitats. Individuals collected in the Ardèche River had back-calculated temperature ranging from 16.9°C to 18.7°C; individuals from the lône de Malaubert from 14.5°C to 21.6°C, and those from the channelized Rhône River (both stations) from 17.5°C to 19.5°C.

4 Discussion

The stable oxygen isotope content of otoliths is widely used to determine the thermal life history of fishes in marine, brackish, and freshwater environments. However, although Cypriniformes fish represent one third of freshwater fish species worldwide (Stout et al., 2016), our study and the one by Burbank et al. (2020) are the only studies to have established the relationship between ambient water temperature and the isotopic signature of *lapilli*. As expected, our study showed a clear fractionation between the otolith $\delta^{18}O$ ($\delta^{18}O_{oto}$)

TABLE 4 Average back-calculated temperatures (±sd) experienced by fish.

	Station 1	Station 2	Station 3	Station 4
	Ardèche River	Lône de Malaubert	Upstream of Tricastin PP	Downsteam of Bollène PP
$T_{weighted}$	17.63 (1.06)	16.81 (0.76)	17.84 (0.51)	19.54 (0.35)
This study	17.76 (0.52)	16.46 (2.37)	18.30 (0.23)	19.33 (0.23)
Burbank et al. (2020)	15.57 (0.59)	14.09 (2.69)	16.18 (0.89)	17.35 (0.26)
Willmes et al. (2019)	14.28 (0.59)	12.82 (2.67)	14.89 (0.88)	16.05 (0.26)
Storm-Suke et al. (2007)	17.81 (0.53)	16.47 (2.43)	18.36 (0.80)	19.42 (0.24)
Thorrold et al. (1997)	26.40 (0.63)	24.83 (2.88)	27.05 (0.95)	28.30 (0.28)
Kim et al. (2007)	22.10 (0.64)	20.51 (2.90)	22.76 (0.95)	24.01 (0.28)
Geffen (2012)	24.78 (0.73)	22.98 (3.31)	25.54 (1.09)	26.97 (0.32)
Godiksen et al. (2012)	16.39 (0.54)	15.05 (2.44)	16.95 (0.80)	18.01 (0.24)
Høie et al. (2004)	23.26 (0.69)	21.56 (3.12)	23.97 (1.03)	25.32 (0.30)
Watkins et al. (2013)	26.65 (0.66)	25.00 (3.01)	27.33 (0.99)	28.64 (0.29)
Holden et al. (2022)	24.33 (0.81)	22.33 (3.39)	25.17 (1.21)	26.77 (0.36)
Kastelle et al. (2022)				
B. saida	18.55 (0.64)	16.97 (2.89)	19.20 (0.95)	20.46 (0.28)
G. macrocephalus	16.62 (0.81)	14.63 (3.69)	17.46 (1.21)	19.06 (0.36)
E. gracilis	20.62 (0.80)	18.64 (3.66)	21.46 (1.20)	23.04 (0.35)
T. chalcogramma	16.70 (0.74)	14.88 (3.35)	17.46 (1.10)	18.91 (0.32)

Temperatures were calculated using the monthly water temperature weighted by fish lifetime ($T_{weighted}$), or back-calculated from the equations obtained from the literature. PP, power plant; *B. saida*, *Boreogadus saida*; *G. macrocephalus*, *Gadus macrocephalus*; *E. gracilis*, *Eleginus gracilis*; *T. chalcogramma*, *Theragra chalcogramma*.

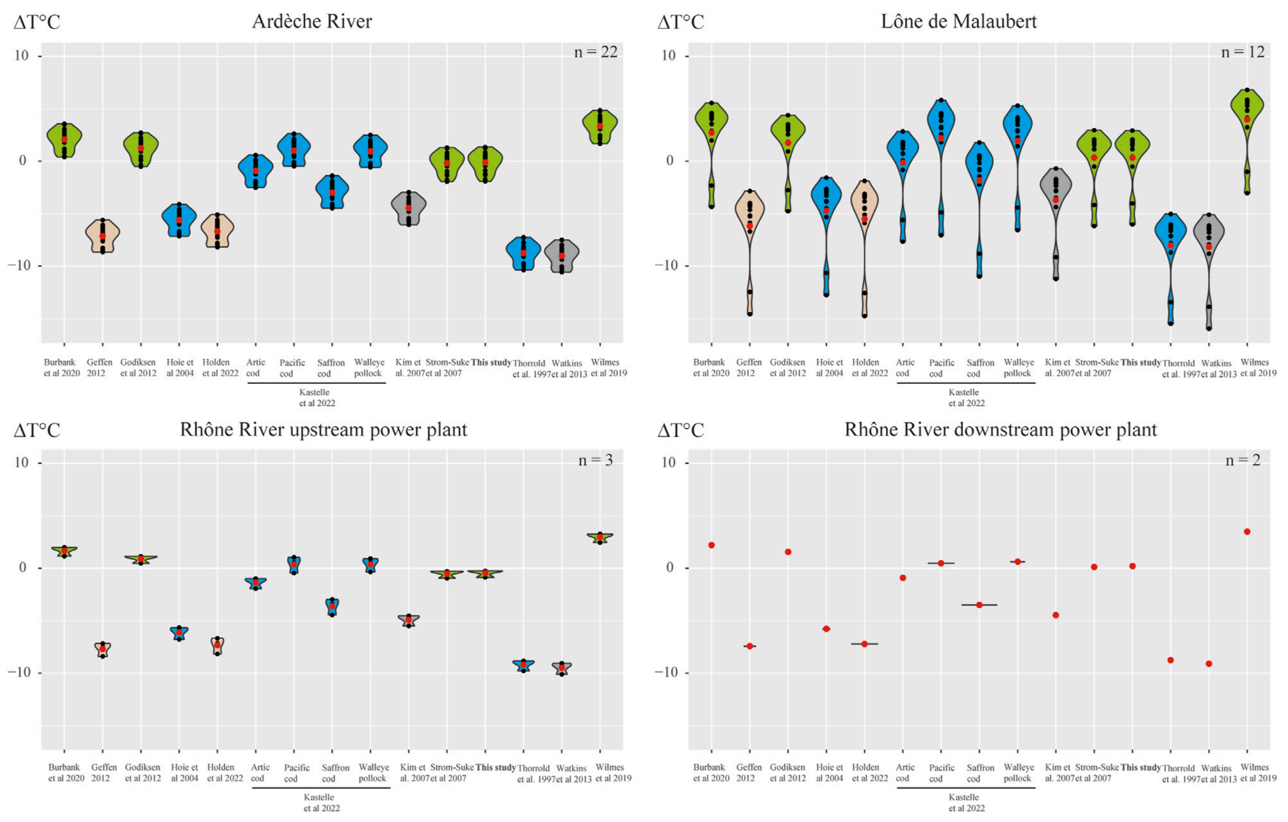

FIGURE 5
Violin plot of ΔT [difference between back-calculated temperature values and mean weighted temperatures ($T^{\circ}C_{weighted}$)]. In green, fish from freshwater environments, in blue from marine environments, in brown from multiple environments (marine, brackish, freshwater) and in gray for *in vitro* experiments. The red dots represent the average values. Artic cod = *Boreogadus saida*, Pacific cod = *Gadus macrocephalus*, Saffron cod = *Eleginus gracilis*, Walleye Pollock = *Theragra chalcogramma*.

and the water $\delta^{18}O$ ($\delta^{18}O_w$) for *lapilli* as a function of temperature. Consequently, we developed a new oxygen fractionation equation specific to European chub. We found that the back-calculated temperature values derived from this equation were in much better agreement with the measured *in situ* temperatures than when using previously published equations.

To test the ability of the approach to identify non-resident (i.e., migrant) individuals, we performed a complementary analysis by back-calculating temperatures from the $\delta^{18}O_{oto}$ signatures of the individuals identified as migrants by Bounket et al. (2021). These individuals showed much greater deviation from the average weighted ambient temperature compared to resident fishes (Supplementary Figure S1). This finding suggests that these individuals inhabited environments with different thermal conditions than the station where they were caught. Furthermore, it highlights how such an approach can help identify resident and migrant individuals, ideally alongside otolith and water microchemical analyses.

4.1 Performance of the fractionation equations

Fractionation equations developed for fish from freshwater environments (Storm-Suke et al., 2007, and the present study; Godiksen et al., 2012; Burbank et al., 2020) showed back-calculated temperatures closer to average weighted temperatures than those developed for fish from marine or brackish environments (Thorrold et al., 1997; Høie et al., 2004; Geffen, 2012; Holden et al., 2022) and from *in vitro* precipitation (Kim et al., 2007; Watkins et al., 2013). Kastelle et al. (2022) have recently proposed four species-specific equations for different marine species (three cod species and one pollock) among which the one for the Arctic cod *Boreogadus saida* (Lepechin, 1774) performed reasonably well in reconstructing the average temperature of the life span of the studied chub juveniles. The chub-specific equation developed in the present study showed the closest back-calculated temperature values (mean difference to $T_{weighted}$ = 0.013°C), closely followed by the equation from Storm-Suke et al. (2007) (mean difference to $T_{weighted}$ = −0.028°C). Values of temperature back-calculated using the equation developed by Burbank et al. (2020) for the freshwater leucicid *Notropis photogenis* underestimated by 2.21°C ± 1.80°C and 2.23°C ± 0.21°C the temperature obtained from the weighted average temperature and from the chub-specific equation, respectively. This was unexpected since this species is the closest relative of the European chub (in terms of phylogeny), for which a fractionation equation has been developed. Both Burbank et al. (2020) and the present study considered the totality of the otolith (*in toto* measurements) and provided an estimation of the temperature for the life span of the fish. However, Burbank et al. (2020) studied 0+ and

1+ fishes, whereas in our study only 0+ fishes, were studied. These differences in fish age [individuals about 6 months old for our study vs. individuals of older than 1 year in the study by Burbank et al. (2020)] have changed the isotopic signatures recorded in otoliths and have therefore induced differences in the estimated temperatures from the equations proposed in each study. It is worth noting that the slope and intercept of the oxygen isotope fractionation equations established for the *sagittae* of freshwater fish are of the same order of magnitude as those we established for the *lapilli* of European chub (Table 2). To further test the generalizability of the fractionation equation developed in the present study, an independent dataset combining the oxygen isotopic signature of water and chub *lapilli* would be needed. These results confirm the necessity 1) of establishing specific equations to provide reliable tools for estimating the thermal habitat used by fish, and 2) of developing experiments under known environmental conditions.

4.2 The consistent signature of $\delta^{18}O$ within a station

Studies demonstrated that $\delta^{18}O_{oto}$ was linked to $\delta^{18}O_w$ and ambient temperature independently of fish growth (Smith and Jones, 2006; Burbank et al., 2018). We also found no significant relationship between $\delta^{18}O_{oto}$, average fish growth, and fish age. The station signature for $\delta^{18}O$ of otoliths and water was very strong, with highly consistent values within each station and highly distinct values between stations (except for the two consecutive stations located on the channelized river section). A notable exception regarding $\delta^{18}O_{oto}$ was two individuals sampled at the lône de Malaubert. They were identified as residents by Bounket et al. (2021) based on otolith microchemistry (strontium and barium), whereas their $\delta^{18}O_{oto}$ values were very different from the other individuals sampled at this station but very similar to the $\delta^{18}O_{oto}$ of individuals sampled in the channelized river section. As juveniles do not seem to be able to move between the lône de Malaubert and the stations located on the channelized river section, we hypothesize that these individuals sampled in the lône spent time in the main channel of the bypassed old Rhône River, whose $\delta^{18}O_w$ is very similar to that of the channelized section (data not provided).

4.3 The promise of stable oxygen isotope analysis of otoliths and the challenges ahead

The congruence between estimated temperatures from the chub-specific equation and the weighted average temperature measured *in situ* confirmed that the oxygen isotope signature of otoliths is a promising tool for studying the thermal life and habitat use of fish. Furthermore, our work has highlighted the ability to study small otoliths and particularly the *lapillus*, of Cypriniformes juveniles, moreover. Several methodological and monitoring aspects should be the objective of future developments. First, a technical gap remains regarding our ability to perform multiple measurements of a single otolith (*i.e.*, to quantify the $\delta^{18}O$ at multiple depths along the otolith radius) in order to get access to several thermal snapshots throughout the life of fish. To the end, promising methods exist, such as micro-milling (Morat et al., 2014) or the use of secondary ion mass spectrometry (SIMS) on samples collected *in situ* (Matta et al., 2013; Helser et al., 2018). In most cases, micro-milling is not adapted to the small size of the otolith (*e.g.*, micro-milling of spots up to 150 μm whereas the studied otoliths are only twice bigger). In our study, we tried the micro-milling approach of 150 μm spots but the *lapilli* were too fragile and systematically broken. The SIMS technique therefore remains the most suitable method for studying the thermal history (or at least for assessing the variability of temperatures experienced during the life of the fish) recorded in small otoliths but it is still underdeveloped (Von Leesen et al., 2021). Overall, multiple measurements would enable 1) a more accurate characterization of the habitats inhabited by the juveniles across their life, and 2) the possibility to consider fishes that are not exclusive residents of a single environment or station. Second, the implementation of a more comprehensive monitoring of water temperature of the sampled areas and of the directly connected habitats would be valuable in order to more accurately define the thermal context and improve our ability to associate back-calculated temperatures with specific local environments.

This study evidence the necessity of developing species-specific equations linking $\delta^{18}O$ of otoliths and temperature. We created the second equation for cyprinid fish that allowed us to calculate the lifetime average temperature of juvenile chubs.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.6084/m9.figshare.22708111.

Ethics statement

Ethical review and approval was not required for the animal study because All relevant international, national, and/or institutional guidelines for the care and use of animals were followed. Fish were sacrificed using anaesthetic overdose (eugenol) in accordance with the European Directive 2010/63/EU. Fish were collected in accordance with the authorisation numbers: 2015-217-004, 2015-229-DDTSE01, 2017-124-DDTSE01 and 2017-165-0007, delivered by the prefectures.

Author contributions

This study was designed by GC, FM, DB, CA, and AM. Field collections were made GC and BB. Otolith analyses were conducted by BB and DB. Statistical analyses were conducted by FM and AM. The manuscript was written by FM, AM, DB, CA, and GC. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that this study received funding from EDF. The funder was not involved in the study design, collection, analysis, interpretation of data, the writing of this article, or the decision to submit it for publication.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2023.1213239/full#supplementary-material

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